

COST-EFFECTIVE RECOVERY OF AN ENDANGERED SPECIES:
THE RED-COCKADED WOODPECKER

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ABSTRACT

A model for the cost-effective recovery for an endangered species is developed and applied to the red-cockaded woodpecker (*Picoides borealis*), an endangered species once abundant in the southeastern United States. There is a finite set of *integer recovery actions* that might be implemented in each time period with the goal of reaching a population target at some future date. The recovery actions include translocation of individuals or breeding pairs from other locations or captive breeding facilities and the construction of artificial nesting cavities. Dynamic programming is used to solve deterministic and stochastic versions of the model. Least cost *recovery plans* are found for the deterministic problem where it is possible to attain a population target with certainty. For the stochastic problem, the least cost, adaptive recovery actions are identified.

BIOGRAPHICAL SKETCH

Ryan Michael Finseth was born in Inglewood, CA. After completing his work at Hudson High School, Hudson, Ohio, in 1997, he entered the University of Virginia in Charlottesville, Virginia. While at the University of Virginia, he completed a double major in Systems Engineering and Economics. He graduated with distinction and received the degree of Bachelor of Science from the University of Virginia School of Engineering and Applied Science in May 2001. In the years following, he worked professionally in Boulder, Colorado and completed a bicycle trip from San Diego, California to San Jose, Costa Rica. In August 2007, he entered the Department of Applied Economics and Management of Cornell University in Ithaca, New York.

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INTRODUCTION

The Endangered Species Act (ESA) of 1973 was seen as providing a critical legal and strategic framework for saving threatened species from extinction. The ESA charged the U.S. Fish and Wildlife Service (FWS) and the National Oceanic and Atmospheric Administration (NOAA) with identifying threatened species and formulating recovery plans that would establish and maintain viable populations.

In the U.S., the environmental movement of the late 19th century and the conservation movement of the early 20th century had the advantage of vast tracts of federally owned land in the western United States where systems of national parks, federal forests, and public lands could be used to preserve wilderness and provide habitat for wildlife. By the mid-20th century, however, federal lands were no longer viewed as sufficient to stem the wave of extinctions resulting from economic growth and development.

Under the ESA, the listing of a species, designation of critical habitat, and the formulation of recovery plans was almost exclusively the domain of ecologists and population biologists. Economists were viewed with suspicion, and in the 1978 case, *Tennessee Valley Authority v. Hill* (437 U.S. 187, 184 (1978)), the U.S. Supreme Court ruled that the ESA required federal officials to “halt and reverse the trend toward species extinction – whatever the cost.” See Brown and Shogren (1998).

Shogren et al. (1999) list 10 reasons why economics should be central to endangered species protection. We have modified their list to reflect the more recent contributions by economists in measuring diversity and allocating scarce conservation resources. Our reasons for including economic analysis in endangered species

management are as follows. (1) The risk of extinction is determined by both economic and biological factors (Clark et al. 2010). (2) Unfortunately, not every species can be saved (Dennis et al. 1991). (3) Biodiversity and the opportunity cost of recovery actions must be measured to make intelligent decisions on habitat preservation (Weitzman 1992, 1993, 1998). (4) Diminishing returns to preservation actions are likely to prevail (Underwood et al. 2008). (5) Economic and ecological interactions might be best understood in a general equilibrium model (Tschirhart 2000). (6) There may be several ways to achieve recovery targets for an endangered species; economists would advocate choosing the least-cost recovery plan (Halsing & Moore 2008). (7) Pro-active decisions should focus on habitat acquisition and the optimal timing of habitat investment depends on changing economic and ecologic conditions (Conrad 2000). (8) When endangered species are found on privately owned land, incentives will likely be needed for the private preservation of habitat (Ferraro et al. 2005). (9) Understanding the economic incentives of government agencies charged with endangered species protection may be as important as understanding the incentives of private land owners (Shogren et al. 1999). (10) Uncertainty about ecosystem and human behavior requires policies that are adaptive if one is to maintain the viability of both an economy and its supporting ecosystem (Baumgärtner & Quaas 2007).

We are tempted to consolidate the above 10 reasons into a single, overarching, reason for incorporating economic analysis into the recovery plans for endangered species: *Recovery resources are scarce and finding the best, feasible recovery strategy is inherently an optimization problem.*

We illustrate the above rationale by formulating a reasonably general model of cost-effective recovery and then apply both deterministic and stochastic specifications to the red-cockaded woodpecker (*Picoides borealis*), a federally listed endangered species that was once abundant in the southeastern U.S. To our knowledge, our model is unique because the underlying recovery actions and the endangered population are discrete integer variables. This leads to a dynamic, combinatorial optimization problem when seeking the least-cost sequence of recovery strategies to achieve a population target at some future date. When recovery costs are discounted, we show that deterministic and stochastic problems can be solved by dynamic programming.

In the next section we provide a justification for our general model by looking at the history of some of the more famous recovery plans for endangered species in the United States. This is followed by the formulation of our general model. We then provide a specification that is well suited to the recovery of the red-cockaded woodpecker (RCW) on the Palmetto Peartree Preserve (3P) in northeastern North Carolina. Both deterministic and stochastic specifications are developed for recovery of the RCW in the 3P. The final section highlights the contribution of this paper and suggests some potential lines for future research.

Some High-Profile Endangered Species in the United States

For many endangered species in the United States, translocation of individuals or breeding pairs from wild populations or breeding facilities (often zoos or government facilities) has played an important role in the recovery or re-establishment of an

extirpated population. Table 1 provides a brief description of translocation and other recovery activities for six, high-profile, endangered species in the United States.

As seen in Table 1, translocation has been used to re-introduce a species to areas where they were extirpated and to increase genetic diversity where an isolated population is showing signs of inbreeding, as with the Florida panther. Other recovery actions are often related to the number of individuals in a population. For the Florida panther and red wolf, vaccination against disease and treatment for parasites has been used to increase the survival of juveniles. For the California condor, “nest watching” and the removal of “microtrash” from the crops of chicks was critical to increasing wild populations in California. When re-establishing the eastern population of whooping crane, ultra light aircraft were used to teach “puppet-reared” juveniles the migratory route from the Necedah Wildlife Refuge in Wisconsin to an over-wintering site in central Florida. For the red-cockaded woodpecker (RCW), translocation has been used to increase both population size and genetic diversity in isolated communities. The construction of artificial cavities has been used to expand the carrying capacity of RCW habitat.

Not reported in Table 1 are estimates of the total expenditures made to re-establish wild populations of these high-profile species. Accurate estimates are difficult to make because recovery efforts often use money and resources from both private (non-profit) conservation groups and federal, state, and local governments. The problem is made more difficult because staff and overhead in both non-profit organizations and government agencies have to be allocated across several activities, only some of which might be dealing with a federally listed species. That said, it was estimated that \$48 million would be needed to fund recovery efforts that might lead to the “de-listing” of the

Table 1. Six high-profile, endangered species in the United States.

U.S. federally listed endangered species	Translocation? (yes/no, comments)	Other recovery actions
Florida panther (<i>Puma concolor coryi</i>)	Yes. In 1995 eight female Texas pumas (<i>Puma concolor stanleyana</i>) were released in south Florida to increase genetic variability.	Vaccination against rabies and feline leukemia. Radio collars to track panthers. Prescribed burning to attract deer and hogs that are prey for the panther. Wildlife (highway) underpasses and fencing to reduce mortality from vehicles on state and interstate highways. Purchase of private land if suitable as panther habitat.
Gray wolf (<i>Canis lupus</i>) in the U.S. northern Rockies	Yes. In 1995, 66 adolescent wolves from packs in the MacKenzie Valley, Alberta, Canada, were released in Yellowstone National Park and in central Idaho.	Radio collars to track movement; few other actions needed. Abundant elk herds within and outside of Yellowstone provided adequate prey for growth of the population now estimated to be 1,650 wolves in Idaho, Montana, and Wyoming. The gray wolf has been de-listed in Idaho and Montana.
Red wolf (<i>Canis rufus</i>) in eastern North Carolina	Yes. Captive breeding programs were established with wolves from a small remnant population along the Gulf Coast of Texas and Louisiana. Listed in 1973, extinct in the wild in the 1980s, the red wolf was re-introduced into the Alligator River National Wildlife Refuge in 1987. Captive red wolf populations exist at 40 facilities in the U.S.	The only wild population is in eastern North Carolina. There is an ongoing program to reduce interbreeding with coyotes. Pups born in captivity are now successfully fostered into wild litters. Wild red wolves are often vaccinated against canine distemper, parvovirus, rabies, heart worm, mange, and other diseases and parasites.
California condor (<i>Gymnogyps californianus</i>)	Yes. The remaining 22 wild California condors were captured in 1987. Two breeding programs were established, one at the San Diego Wild Animal Park and the other at the Los Angeles Zoo. In 1991 and 1992 condors were released in California. In 1996 condors were released on the north rim of the Grand Canyon. There are now four wild populations: at the Grand Canyon, at Zion National Park, in central coastal California, and in northern Baja California. The wild population is estimated at 180 with a captive population of about 170.	Safe carrion (poison- and lead-free) is often placed in areas where condors have been released. Hunters in areas with wild condors cannot use lead bullets. Captive birds have been conditioned to avoid power lines before being released. Captive and wild condors are vaccinated against West Nile Virus. "Nest-guarding," to prevent parents from feeding chicks "microtrash" (small pieces of glass, metal, ceramics, or plastic). Microtrash is removed from the crops of chicks, by surgery, if necessary.
Whooping crane (<i>Grus americana</i>)	Yes. Listed in the U.S. in 1973 and in Canada in 1978. The western population migrates from nesting grounds in the Wood Buffalo National Park in Alberta, Canada, to over-winter in the Aransas Wildlife Refuge along the Gulf coast in Texas. In 1993 a non-migratory flock was established in Kissimmee, Florida. In 2001 an eastern migratory population was established. The eastern population nests in the Necedah Wildlife Refuge in central Wisconsin and over-winters in central Florida. There are approximately 262 cranes in the western migratory population and 103 cranes in the eastern migratory population. The non-migratory population in Kissimmee contains about 30 cranes.	In the 1980s, eggs from the western migratory population, were placed in nests of the sand hill crane (<i>Grus canadensis</i>). Chicks that were raised by sand hill cranes did learn to migrate, but failed to mate with other whooping cranes because they had imprinted on their foster parents. The sand hill crane "fostering project" was discontinued in 1989. An eastern migratory population was established by "costume rearing" chicks from the captive population and teaching them to follow ultralight aircraft on migrations between Wisconsin and Florida. Costume-reared juveniles are also released in autumn, just as the wild whoopers in the eastern flock are about to start their southern migration.

Red-cockaded
woodpecker (*Picoides
borealis*)

Yes. The red cockaded woodpecker (RCW) was listed in 1973. In the 19th century, the species was widely distributed across the southeastern United States. After hatching, chicks are fed by a family group that includes the breeding pair and one or more helpers. RCW require nesting cavities in old growth pine; longleaf pine being preferred. Today there are RCW populations in 11 states on federal, state, and private land. Translocation of breeding pairs from populations at or near carrying capacity has been used to increase populations in areas with excess capacity and to increase genetic variability.

In addition to translocation, the creation of artificial cavities helps to maintain family units and allows the best use of available habitat. Other measures include prescribed burning to prevent “hardwood encroachment” and the use of “restrictor plates” to prevent predators from gaining access to the nest. Restrictor plates also prevent enlargement by other species that compete with the RCW for tree cavities.

whooping crane (USFWS 1994). The Florida panther recovery plan was estimated to cost \$17.75 million for five years, 2008 – 2012 (USFWS 2008). Tobin and Dusheck (2005) estimated that the red wolf recovery plan cost \$1 million per year since 1974. Estimates of the per-wolf cost of re-introduction to Yellowstone and Idaho range from \$200,000 to \$1,000,000 (Daley & Trevis 2005). The cost per year to save the California condor has been estimated at \$5 million (Barlow 2008).

Translocation, by its very nature, is an integer-valued activity. Because other recovery activities are often oriented toward individuals in an endangered population, they too may be integer variables. Integer choice variables make finding the best recovery plan more difficult because the combination of activities constituting a recovery strategy in a given period will scale exponentially over the recovery horizon. For example, in our specification for the RCW, there can be up to six translocated breeding pairs to the Palmetto Peartree Preserve in any period so that $X_{1,t} \in \{0,1,2,3,4,5,6\}$. Let the recovery horizon be $t = 0,1,2,...,T - 1$. In addition, up to 10 artificial cavities can be constructed in each period so that $X_{2,t} \in \{0,1,2,3,4,5,6,7,8,9,10\}$. Suppose that $T = 10$. Then, there are $7 \times 11 = 77$ possible combinations of the two recovery actions that define

a *recovery strategy* for each period. With 10 periods in the recovery horizon there are $77^{10} \gg 7.32668 \times 10^{18}$ possible *sequences* of recovery strategies. A sequence of recovery strategies can be thought of as a recovery plan.

The General Model

Suppose there are $i = 1, 2, \dots, I$ actions that might be employed to hasten the recovery of an endangered species on a preserve owned by a government or conservation organization. We will assume that all recovery actions are discrete (integer) and have a maximum upper bound. Let $X_{i,t} \in \{0, 1, 2, \dots, X_{i,MAX}\}$ denote the discrete choice set for the i^{th} recovery action in period t . We will designate the number of individuals or breeding pairs translocated in period t by $X_{1,t}$. Other actions, $i \neq 1$, might increase carrying capacity on the property or reduce mortality from predators or disease. For example, the re-establishment of the bald eagle in New York State was accomplished by “hacking;” where eaglets, taken from nests in Alaska, were reared in confinement until they could be released, often onto nesting platforms placed in suitable habitat, such as the Montezuma Wildlife Refuge at the northern end of Cayuga Lake.

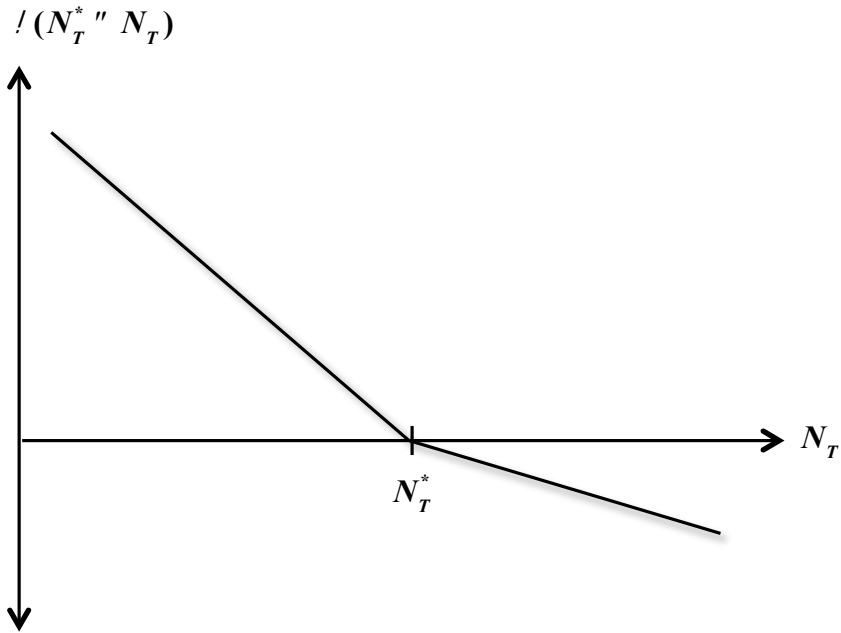
The dynamics of an endangered species might be modeled as a stochastic map. Let $N_t \geq 0$ denote the number of individuals or breeding pairs in the preserve in period t . The population in $t + 1$ is a realization of the stochastic map, $N_{t+1} = F(N_t, K_t, S_t; e_{t+1})$, where K_t is the preserve’s carrying capacity in period t , (discussed in greater detail below), $S_t = [X_{1,t}, X_{2,t}, \dots, X_{I,t}]$ is the recovery strategy in period t , and e_{t+1} is an

independently and identically distributed (*iid*) random variable from the known

distribution, $\tilde{f}(e_{t+1})$. There are $\tilde{O}_{i=1}^I (X_{i,MAX} + 1)$ possible recovery strategies in period t .

Let N_T^* be a recovery target in the terminal period $t = T$. In the stochastic problem we seek the sequence of recovery strategies, $\{S_t\}_{t=0}^{t=T-1}$, or recovery plan, that will minimize the discounted cost of recovery actions over the interval $t = 0, 1, 2, \dots, T - 1$ plus the discounted penalty (reward) for failing to reach (exceeding) the target. The penalty function may be written as $j(N_T^* - N_T)$, where $j(N_T^* - N_T) > 0$ if $N_T^* - N_T > 0$, $j(N_T^* - N_T) = 0$ if $N_T^* - N_T = 0$, and $j(N_T^* - N_T) < 0$ if $N_T^* - N_T < 0$. A possible shape for the penalty function is shown in Figure 1. As we will see, realized population levels in $t = T$ that exceed the recovery target serve to reduce the discounted cost of recovery strategies.

Figure 1. The penalty function in the terminal time period, $t = T$.



Carrying capacity, K_t , might be enhanced by some of the actions. This leads to a second, deterministic map $K_{t+1} = \min[G(K_t, S_t), K_{MAX}]$, implying that carrying capacity in period $t + 1$ is the minimum of $K_{t+1} = G(K_t, S_t)$ or K_{MAX} , interpreted as the maximum carrying capacity when the preserve has been “fully enhanced.”

Let the cost of strategy S_t be given by a function $C(S_t)$. Let $r = 1/(1 + d)$, be a discount factor, where $d > 0$ is the rate of discount. Then, our dynamic, optimization problem seeks to

$$\begin{aligned}
 \underset{\{S_t\}_{t=0}^{t=T-1}}{\text{Minimize}} \quad & C = \sum_{t=0}^{t=T-1} r^t C(S_t) + r^T j(N_T^* - N_T) \\
 \text{Subject to} \quad & N_{t+1} = F(N_t, K_t, S_t; e_{t+1}), N_0 \geq 0 \text{ given,} \\
 & K_{t+1} = \min[G(K_t, S_t), K_{MAX}], K_0 \geq 0 \text{ given,} \\
 & S_t = [X_{1,t}, X_{2,t}, \dots, X_{I,t}] \\
 & X_{i,t} \in \{0, 1, 2, \dots, X_{i,MAX}\}, i = 1, 2, \dots, I \\
 & f(e_{t+1}) \text{ known, } T > 0 \text{ given}
 \end{aligned}$$

In the deterministic problem, the stochastic map for the endangered species is replaced by a deterministic map, $N_{t+1} = F(N_t, K_t, S_t)$. In the deterministic model the penalty function is dropped because it is possible to determine all feasible values of $N_T = N_T^*$. We will elaborate on this point in the application to the red-cockaded woodpecker.

The Red-Cockaded Woodpecker

Red-cockaded woodpeckers are the primary excavators of tree cavities used by at least 27 vertebrate species (USFWS 2003). Degradation and loss of longleaf pine habitat in the southeastern United States has led to severe declines in RCW populations. In addition, existing populations are highly fragmented and often isolated from other populations

(Conner et al. 2001). As a result, habitat conservation and management are crucial to the continued viability of the RCW.

The red-cockaded woodpecker has been the focus of numerous research efforts over the past thirty years and much is known about the species' population dynamics and habitat requirements. Red-cockaded woodpeckers are cooperative breeders. They live in breeding groups consisting of a breeding pair and up to four helpers. These helpers forego reproduction and assist in raising the group's fledglings until they are able to fill a breeding vacancy in their current (or an adjacent) breeding group. RCW breeding groups occupy a territory consisting of nesting and foraging habitat and will typically cover 40 to 160 hectares (USFWS 2003). The size of this territory is usually dependent on the quality of the habitat; territories in relatively poor quality habitat are larger than territories located in higher quality habitat (Walters et al. 2000). The quality of the habitat depends on a number of factors including tree species, stand age, tree density, and the presence of herbaceous groundcover.

Each RCW territory contains a collection of cavity trees, called a cavity cluster, and each group member occupies its own cavity (Walters et al. 1988). The construction of each cavity takes many years (Conner & Rudolph 1995). Due to the significant time required to construct a cavity, new territory creation is slow and tedious. Therefore it is advantageous for an individual woodpecker to compete to fill a breeding vacancy in an existing territory, or to colonize a suitable, unoccupied territory.

The number of suitable territories (occupied and unoccupied) comprising a population is referred to as the population's carrying capacity. A decrease in carrying capacity occurs when a cluster becomes unsuitable for occupation and is often the result

of cavity tree mortality, cavity enlargement (most commonly by pileated woodpeckers), cavity kleptoparasitism, and/or hardwood mid-story encroachment (Conner & Rudolph 1989).

Some interesting population dynamics arise from the cooperative breeding behavior of the RCW. The existence of a large non-breeding class (helpers) serves to buffer variations in breeder mortality or fecundity (Connor et al. 2001; Walters et al. 2002). The size of the breeding population is not severely affected by a decline in the number of fledglings or increases in breeder mortality. As a result, the number of breeding pairs is commonly used as the measure of RCW population size (USFWS 2003). In addition, because new territory creation in most instances is rare, the number of breeding pairs is often limited to the population's carrying capacity. These dynamics have important implications for RCW management. Because the RCW breeding class is not strongly affected by demographic stochasticity, management activities that aim to alter rates of fecundity or mortality will have little effect on the number of breeding pairs (Rudolph et al. 2003). Finally, because the number of breeding pairs in a population is limited by the carrying capacity, the most effective way to increase the number of breeding pairs is to increase the carrying capacity (Rudolph et al. 2003).

Research has resulted in a suite of management activities that are currently employed to maintain and enhance RCW habitat. These include but are not limited to translocation, artificial cavity construction, and prescribed burning. Translocation involves the non-natural movement of an individual RCW from within or between populations (USFWS 2003). The use of translocation has multiple benefits; it serves to augment the size of the destination population and helps to increase genetic diversity

among the destination population. Artificial cavity construction involves the drilling (or installation) of artificial cavities in desired locations. Artificial cavities allow managers to replace cavities lost due to tree mortality or kleptoparasitism, and/or create new cavity clusters/territories in previously unoccupied habitat. Territories constructed in previously unoccupied habitat should be located within 3 kilometers of an occupied territory (in order to facilitate colonization) and include at least four artificial cavities (to create a cavity cluster) (USFWS 2003). Prescribed burning is a management activity that can effectively control hardwood encroachment and improve foraging habitat (USFWS 2003). Our analysis focused solely on translocation and artificial cavity construction because the effects of these management actions are straightforward to quantify.

Red-Cockaded Woodpecker Recovery

Due to current timber management practices and the alteration of the fire regime, virtually all red-cockaded woodpecker populations require management in the short term to remain viable. Rudolph et al. (2004) describe management techniques available to RCW land managers and offer a strategy for short term, cost-effective recovery based on years of research into RCW population dynamics. Rudolph, Conner, and Walters argue that the decline in RCW habitat carrying capacity is the primary reason for the decline in RCW potential breeding groups (the typical measure of RCW population health) and that most populations, even those in decline, contain a level of potential breeding groups at or near carrying capacity. In the case of the RCW, carrying capacity is relatively easy to determine; it is equal to the number of cavity clusters (nesting sites) available in suitable habitat. The authors advocate for the use of management techniques aimed at

maintaining or increasing carrying capacity: (1) prescribed burning should be employed to in order to keep nesting and foraging habitat suitable; (2) artificial cavities should be constructed to replace cavities lost due to cavity tree mortality in order to maintain the number of suitable cavity clusters and, consequently, the carrying capacity; and (3) artificial cavities should be constructed in previously unoccupied habitat to increase carrying capacity.

Rudolph et al. also argue that management techniques intended to increase fecundity rates or decrease mortality rates are ineffective at increasing the number of RCW potential breeding groups. They argue that these techniques will result in an increased number of individual birds (non-breeding helpers in particular), but are not effective in increasing the number of potential breeding groups within a population. Because of this, control of predators and kleptoparasitism (invasion of cavities by other species) are not recommended management actions.

The strategy advocated by Rudolph et al. present land managers with management actions that are the most effective at achieving an increase in the number of potential breeding groups. Their analysis, however, does not provide information on the magnitude of the effects that the recommended management techniques on RCW populations, nor provides information on the economic cost of each technique. In order to evaluate the cost-effectiveness of RCW management actions, it will be necessary to attempt to quantify the effectiveness of each action in achieving a recovery goal and compare that to its economic cost.

Population Models

The cooperative breeding behavior of the red-cockaded woodpecker renders their population dynamics difficult to model with standard Leslie matrix models. Heppel et al. (1994) developed a deterministic, stage-based matrix model of RCW population dynamics. Field data from the North Carolina Sandhills was used to parameterize the survival and transition probabilities in the six stage model. The authors use the qualitative results of the model to evaluate the effects of five management techniques on red-cockaded woodpecker populations.

To evaluate the effectiveness of management techniques, the effect of each technique on the survival and transition probabilities was predicted: (1) deterring kleptoparasitism was predicted to increase fecundity; (2) the translocation of females was predicted to increase the transition from solitary males to breeding males; (3) increasing cavities in occupied territories was predicted to increase the fledgling to helper transition probability, consequently decreasing the fledgling to breeder transition; (4) increasing new territory establishment was predicted to increase fledgling to breeder and helper to breeder transition probabilities and decrease fledgling mortality; (5) improving foraging habitat was predicted to decrease mortality. Population effects can be calculated by multiplying the matrix attributes' elasticities (the proportional sensitivity of intrinsic rate of increase to change in model parameter) by proportional increases in the parameters that are predicted to be affected by management. The authors conclude that techniques aimed at increasing fecundity and decreasing mortality serve only to increase the number of individuals, and only techniques that increase carrying capacity will help to increase the number of breeders in the population.

To account for the importance of spatial dynamics in RCW population viability, Letcher et al (1998) present a spatially explicit, individual-based model of RCW population dynamics. Specifically, the model accounts for the variation in population dynamics arising from unique territory distributions across the landscape. The parameter estimation of this model relied on the same field data from the North Carolina Sandhills used in the parameterization of stage-based matrix model discussed above.

The authors ran multiple model simulations, varying the number of territories (25, 49, 100, 169, 250, or 500) and the spatial distribution of territories (clumped or dispersed). Results revealed that populations of 250 or greater were persistent and populations less than 50 declined regardless of their spatial distribution. Populations greater than 50 and less than 250 were persistent when highly aggregated across the landscape (clumped) and declined when dispersed across the landscape.

The model has been incorporated into the RCW DSS, an ArcGIS plug-in, wherein managers can run simulations using shapefile inputs containing land cover data and the locations of RCW territory clusters. In addition to providing useful insights into the viability of individual populations, the RCW DSS is also a valuable tool when analyzing the potential effects of new RCW territory creation, or recruitment clusters. The RCW DSS allows land managers to input the location of recruitment clusters as well as the year in which they will be created. Users can compare population levels with and without recruitment clusters in order to evaluate the efficacy of the recruitment cluster(s). However, the RCW DSS does not account for the effects of other management actions, including cavity replacement, translocation, and prescribed burning. In addition, the RCW DSS will remove a territory from the landscape if it has been unoccupied for five

years. This functionality is not consistent with a managed territory wherein all managed territories should remain suitable.

METHODS

The Red-Cockaded Woodpecker in the Palmetto Peartree Preserve

The Conservation Fund established The Palmetto Peartree Preserve (3P) in northeastern North Carolina in 1999 and now serves as an RCW support population. We solved the following specification of the general, cost-effective, recovery problem.

$$\begin{aligned}
 \text{Minimize } C &= \sum_{t=0}^{t=T-1} r^t C(S_t) + r^T j(N_T^* - N_T) \\
 \text{Subject to } N_{t+1} &= e_{t+1} \{sX_{1,t} + (1+r-rN_t/K_t)\}N_t \\
 K_{t+1} &= \min[(1-a)K_t + X_{2,t}, K_{MAX}] \\
 X_{1,t} &\in \{0, 1, 2, \dots, X_{1,MAX}\} \\
 X_{2,t} &\in \{0, 1, 2, \dots, X_{2,MAX}\} \\
 K_t &\geq N_t \\
 K_0 &\geq 0, N_0 \geq 0 \text{ given.}
 \end{aligned}$$

In the above specification the two recovery actions are translocation of breeding pairs $X_{1,t}$, and the construction of artificial cavities $X_{2,t}$. Both are integer variables with constant marginal costs given by $c_1 > c_2 > 0$, respectively. In addition, artificial cavity construction requires the construction of four cavities comprising an entire artificial cavity cluster.

The penalty function is $j(N_T^* - N_T) = \$Q(N_T^* - N_T)$ if $N_T^* \geq N_T$ and $j(N_T^* - N_T) = \$R(N_T^* - N_T)$ if $N_T^* \notin N_T$. The first-period survival of a translocated breeding pair is $1 > s > 0$, $r > 0$ is the intrinsic growth rate for established breeding pairs,

and K_t is the carrying capacity measured by the number of cavity clusters suitable for occupancy. The number of cavity clusters can decrease over time if they are occupied by another species, encroached by hardcover growth, or if the tree containing the cavity is felled by insect infestation, wind, or disease.

The number of RCW cavity clusters (or territories) is subject to an upper bound, K_{MAX} , based on the nesting and foraging habitat required for each breeding pair. Cavity clusters become unsuitable at rate $1 > \alpha > 0$, and require the construction of four artificial cavities to become suitable for colonization. This results in the map

$K_{t+1} = \min[(1 - \alpha)K_t + X_{2,t}, K_{MAX}]$. In each period the number of cavity clusters must equal or exceed the number of nesting pairs, $K_t \geq N_t$.

We used dynamic programming to solve the deterministic and stochastic instances of our dynamic, combinatorial optimization problem. The state variables in the model are the integer values for carrying capacity, K_t , and the number of breeding pairs, N_t , where $0 \leq K_t \leq K_{MAX}$, $0 \leq N_t \leq K_{MAX}$, and $K_t \geq N_t$ for all $t = 0, 1, 2, \dots, T - 1$. The state transition functions frequently do not generate integer values for K_{t+1} and N_{t+1} , therefore it was necessary to define probability weights for future states. In the stochastic instance, we used bilinear interpolation to force K_{t+1} and N_{t+1} to be integers (see Appendix S1). In the deterministic instance, we rounded non-integer values of K_{t+1} and N_{t+1} to the nearest integer.

We have provided the Matlab code used to solve the stochastic problem with the above penalty function and where the random variable, e_{t+1} , is drawn from a discrete distribution where $\Pr(e_{t+1} = 0.75) = 0.25$, $\Pr(e_{t+1} = 1.00) = 0.50$, and

$\Pr(e_{t+1} = 1.25) = 0.25$ in Appendix S2. The code provided permits users to specify more than 3 discrete values for the random variable, $e_{t+1}, \varepsilon_{t+1}$.

Parameters

The Conservation Fund provided yearly data on carrying capacity and RCW breeding pairs from 1999 to 2008. We used non-linear least squares analysis to estimate the value of the intrinsic growth rate, $r = 0.13$. The upper bound on carrying capacity K_{MAX} was calculated by dividing the amount of suitable habitat by the average size of the home range of an RCW breeding pair (approximately 50 hectares). Connor et al. (1991) estimated the annual cavity tree mortality rate of loblolly pine (the most abundant species in 3P) to be 0.06. We set the annual rate of decline in carrying capacity, $a = 0.10$, a value significantly greater than the annual cavity tree mortality rate in order to account for additional cavity losses due to kleptoparasitism, and hardcover encroachment. Our model required a specific criterion be met for the translocation to be considered a success; both translocated individuals must have remained at the target cluster, followed by pairing and nesting. Previous estimates for the translocation success rate of RCW breeding pairs ranged from 33% (Costa & Kennedy 1994) to 13% (Edwards & Costa 2004). In this analysis, we set $s = 0.25$ as it lies within the previously reported range. The United States Fish and Wildlife Service (2003) determined the cost of translocating one breeding pair, c_1 , to be \$3000, and the cost of constructing one artificial cavity cluster, c_2 , to be \$800. We assigned the penalty parameter in the final function to be $Q = \$40,000$, and the bonus parameter to be $R = \$5,000$. The penalty parameter needed

Table 2. Description and estimate of parameters for the deterministic and stochastic problem specifications of red-cockaded woodpecker recovery in the Palmetto Peartree Preserve.

Parameter	Description	Value
r	Intrinsic growth rate	0.13
s	Translocation success rate	0.25
a	Rate of decrease in carrying capacity due to cavity tree mortality, hardcover encroachment, kleptoparasitism, etc.	0.10
K_{MAX}	Upper bound on carrying capacity	50
$X_{1,MAX}$	Upper bound on the number of breeding pairs to be translocated per time period	6
$X_{2,MAX}$	Upper bound on the number of artificial cavity clusters to be constructed per time period	10
N_0	Number of breeding pairs at time $t = 0$	30
K_0	Number of managed cavity clusters at time $t = 0$	30
c_1	Cost of translocating one breeding pair	\$3,000
c_2	Cost of constructing one artificial cavity cluster (four tree cavities)	\$800
e_{t+1}	Random variable	$\Pr(e_{t+1} = 0.75) = 0.25$ $\Pr(e_{t+1} = 1.00) = 0.50$ $\Pr(e_{t+1} = 1.25) = 0.25$
d	Discount rate	0.05
r	$1/(1 + d)$	0.95
T	Time horizon	10
N_T^*	Population Target	42
Q	Unit penalty when $N_T < N_T^*$	\$40,000
R	Unit bonus when $N_T > N_T^*$	\$5,000

to be sufficiently large relative to the cost of $X_{1,MAX}$ and $X_{2,MAX}$ for the penalty to have “bite.” Numerically, for the penalty function to be an appropriate disincentive one would want $Q > c_1 X_{1,MAX} + c_2 X_{2,MAX}$. Finally, we assigned a positive discount rate, $d = 0.05$, a

time horizon, $T = 10$, and a population target in the stochastic problem, $N_T^* = 42$. We have provided a summary of parameter estimates in Table 2.

RESULTS

We solved the deterministic problem where $\Pr(e_{t+1} = 1.00) = 1$. In the deterministic problem, the penalty function is unnecessary because we used dynamic programming to solve for the least cost sequence of recovery plans that will precisely reach a feasible target, N_T^* . Given the initial conditions, $N_0 = 20$ and $K_0 = 30$, the set of feasible population targets greater than our initial population is $\{21, 22, \dots, 47\}$. We determined the upper bound by running the population model with the values of all recovery actions set equal to their maximum in each year, $X_{1,t} = X_{1,MAX}$ and $X_{2,t} = X_{2,MAX}$, where $t = 0, 1, 2, \dots, 9$. We generated optimal (least-cost, present value) recovery plans, $\{S_t\}_{t=0}^{t=T-1}$, for all feasible population targets in the deterministic problem. We have presented the least cost recovery plans for the population targets $N_T^* = 42, 43, \dots, 47$ in Table 3. We also calculated the discounted total cost of the least cost recovery plan,

$C^* = \mathring{a}_{t=0}^{t=T-1} r^t [c_1 X_{1,t}^* + c_2 X_{2,t}^*]$, for every feasible population target. The discounted total cost of the least cost recovery plans are increasing in N_T^* (Fig. 2).

The least cost recovery plan for a population target $N_T^* = 42$ and a zero discount rate ($d = 0$) is $X_1^* = \{3, 6, 1, 0, 0, 0, 1, 1, 1, 6\}$ and $X_2^* = \{8, 10, 10, 7, 5, 5, 5, 5, 4, 0\}$. The least cost recovery plan with an identical population target and a positive discount rate ($d = 0.05$) is $X_1^* = \{0, 2, 1, 0, 0, 0, 0, 5, 5, 6\}$ and $X_2^* = \{7, 10, 10, 6, 6, 6, 2, 8, 4, 0\}$. With a

positive discount rate, the majority of translocations are delayed until the final three years of the time horizon. Discounting provides incentive to delay the adoption of costly recovery actions.

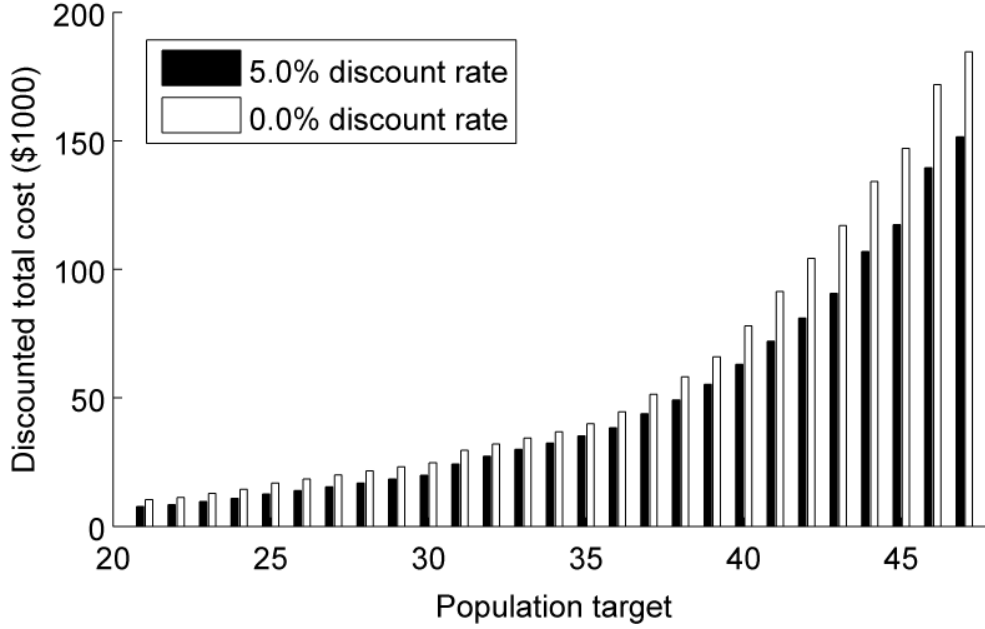
Table 3. The least cost recovery actions, $X_{1,t}^*$ and $X_{2,t}^*$, for all $t = 0, 1, 2, \dots, T-1$, and $N_T^* = 42, 43, \dots, 47$.

t	$N_T^* = 42$		$N_T^* = 43$		$N_T^* = 44$		$N_T^* = 45$		$N_T^* = 46$		$N_T^* = 47$	
	$X_{1,t}^*$	$X_{2,t}^*$	$X_{1,t}^*$	$X_{2,t}^*$	$X_{1,t}^*$	$X_{2,t}^*$	$X_{1,t}^*$	$X_{2,t}^*$	$X_{1,t}^*$	$X_{2,t}^*$	$X_{1,t}^*$	$X_{2,t}^*$
0	0	7	0	7	3	7	3	7	3	8	3	8
1	2	10	2	10	2	10	2	10	2	10	6	10
2	1	10	1	10	1	10	1	10	5	10	5	10
3	0	6	0	6	0	6	0	6	4	6	4	7
4	0	6	0	6	0	6	4	7	4	3	4	3
5	0	6	0	6	4	3	4	3	5	8	5	7
6	0	2	4	3	5	8	5	7	5	4	5	5
7	5	8	5	7	5	4	5	5	6	5	6	5
8	5	4	5	5	6	5	6	5	3	5	3	5
9	6	0	6	0	3	0	3	0	4	2	4	2

To solve the stochastic instance we employed the penalty function because it was not possible to guarantee that all feasible population targets could be reached with certainty. Further, due to the randomness of e_{t+1} , we were unable to predetermine least cost recovery plans at time $t = 0$. Therefore, the least cost recovery strategies must be adaptive because the least cost recovery actions, $X_{1,t}^*$ and $X_{2,t}^*$, are conditional on N_t , K_t , and t , $[X_{1,t}^*, X_{2,t}^* | N_t, K_t, t]$. We used a customized, stochastic, dynamic programming algorithm to determine the least cost, adaptive recovery actions, $X_{1,t}^*$ and $X_{2,t}^*$, for all

feasible combinations of N_t and K_t for all $t = 0, 1, 2, \dots, T - 1$. See Appendix S2 for the Matlab code for our stochastic dynamic program.

Figure 2. Minimum discounted cost required to precisely achieve the population target, N_T^* , in the deterministic problem specification.



We limit our discussion to the optimal (least cost, present value) decision rules for translocation in time $t = 0$ and $t = 9$, $X_{1,0}^*$ and $X_{1,9}^*$, for a population target, $N_T^* = 42$. The optimal number of translocations depends primarily on the number of breeding pairs in the population in time t and is almost exclusively either $X_{1,t}^* = X_{1,MIN} = 0$ or $X_{1,t}^* = X_{1,MAX} = 6$, denoted by the black and light grey shaded grid cells, respectively, in Figure 3. If the number of breeding pairs in time t exceeds a certain population threshold, the optimal number of translocations is $X_{1,t}^* = X_{1,MIN} = 0$. However, if the number of breeding pairs in time t falls short of the same population threshold, the optimal number of translocations is $X_{1,t}^* = X_{1,MAX} = 6$. The population threshold is

increasing in t . There are exceptions to this general decision rule, however. If the number of breeding pairs is equal to the population threshold, the optimal number of translocations will also depend on the carrying capacity in time t . The population threshold in the initial time period, $t = 0$, is 14 breeding pairs (Fig. 3a), and in final time period, $t = 9$, the population threshold is 42 breeding pairs (Fig. 3b). Therefore, if the number of breeding pairs in the final time period is less than the population target, $N_T^* = 42$, the optimal decision rule is to perform the maximum number of translocations.

Concurrently, we found optimal decision rules for the number of artificial cavity clusters constructed in time $t = 0$ and $t = 9$, $X_{2,0}^*$ and $X_{2,9}^*$, for a population target, $N_T^* = 42$. In the initial time period, it is optimal to construct the maximum number of artificial cavity clusters, $X_{2,t}^* = X_{2,MAX} = 10$ (denoted by the light grey grid cells in Figure 4a), for the majority of feasible states. However, if the number of breeding pairs is small relative to the number of available cavity clusters, it is optimal to construct fewer artificial cavity clusters. As one approaches the terminal time period, $t = T$, the optimal number of artificial cavity clusters constructed decreases for the majority of feasible states until in time $T - 1$ cavity clusters are constructed only for those feasible states where the number of breeding pairs is equal to or nearly equal to carrying capacity (Fig. 4b).

Figure 3. Optimal number of translocations, $X_{1,t}^*$, for population target, $N_T^* = 42$, in (a) $t = 0$; (b) $t = 9$.

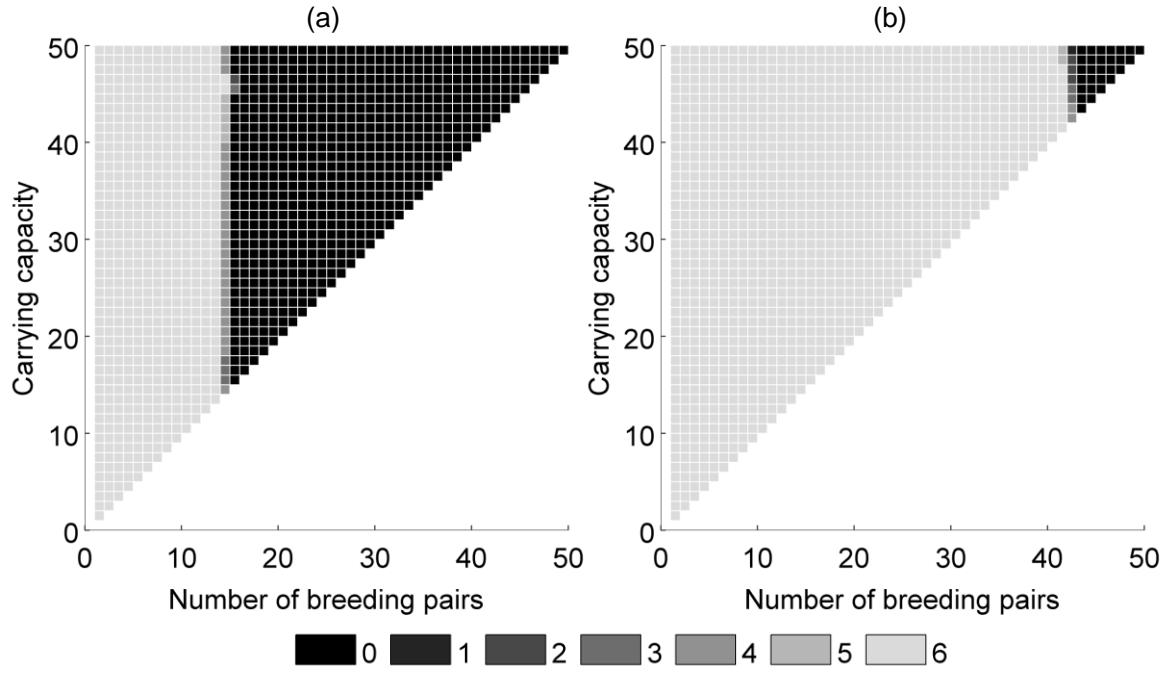
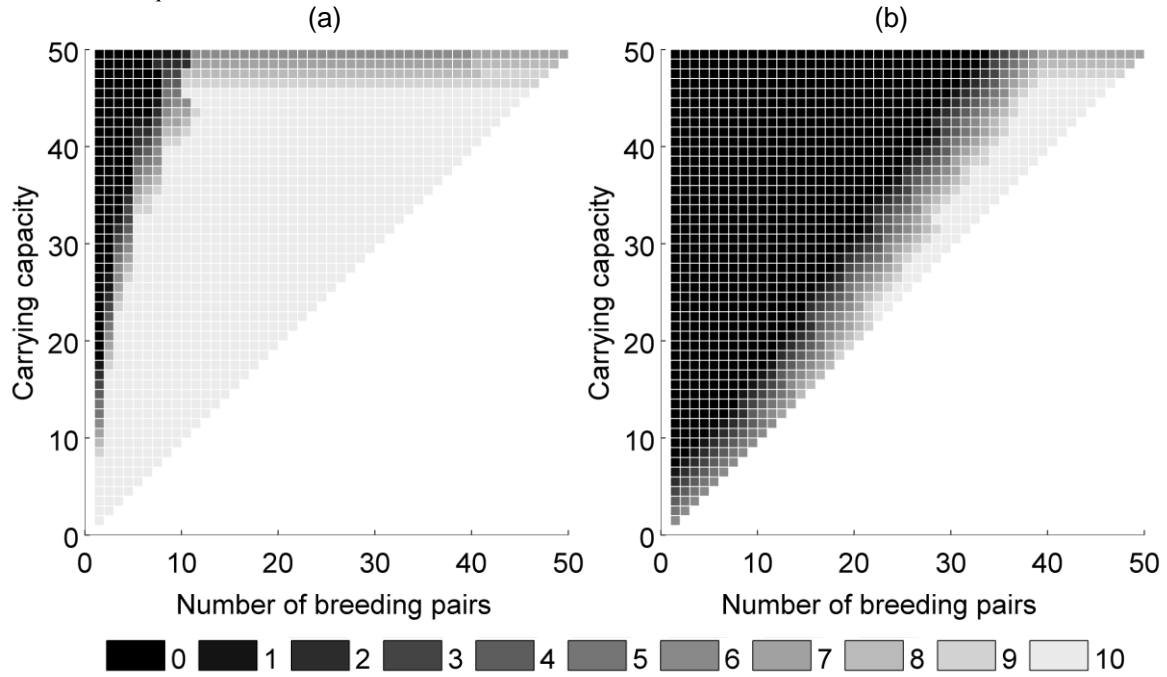
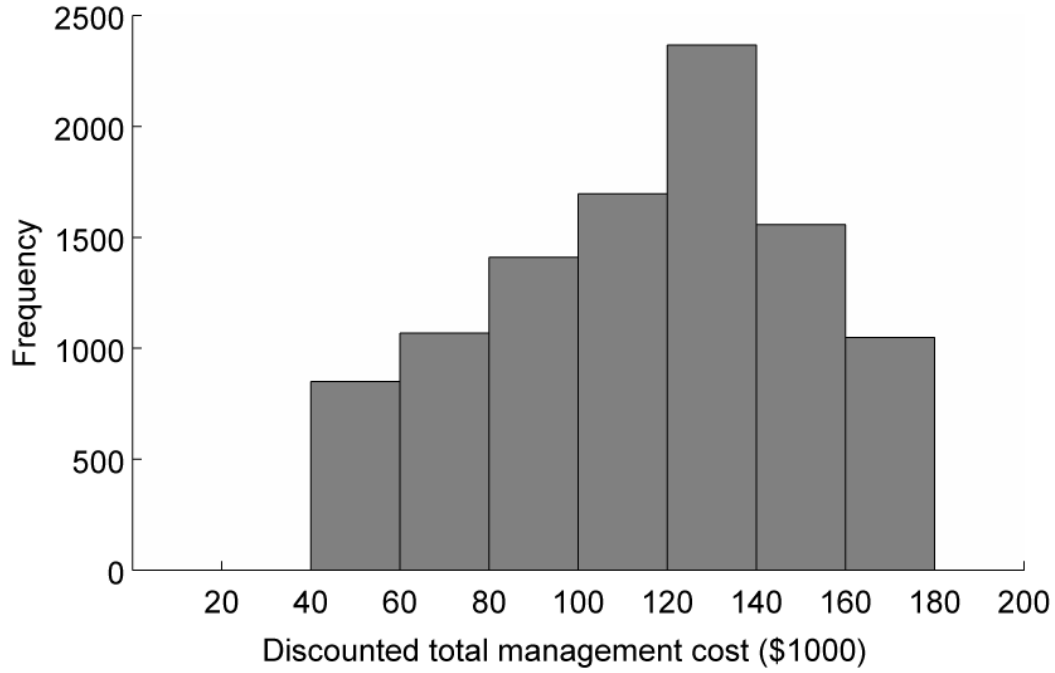


Figure 4. Optimal number of artificial cavity clusters constructed, $X_{2,t}^*$, for population target, $N_T^* = 42$, in (a) $t = 0$; (b) $t = 9$.



We used the least cost, adaptive recovery actions, $X_{1,t}^*$ and $X_{2,t}^*$, output from our model to generate 10,000 realizations of the stochastic model. Discounted total management cost, $C^* = \sum_{t=0}^{t=T-1} r^t [c_1 X_{1,t}^* + c_2 X_{2,t}^*]$, for these adaptive recovery strategies when $N_T^* = 42$, ranged from a minimum of \$45,251 to a maximum of \$173,190 with an average total management cost of \$115,430 (Fig. 5).

Figure 5. Distribution of discounted total management cost for population target, $N_T^* = 42$, based on 10,000 realizations.



DISCUSSION

The Endangered Species Act of 1973 states that recovery plans should be developed and implemented for all endangered and threatened species, unless a recovery plan would not aid in the conservation of the species. These recovery plans include descriptions of site-specific management activities, objective criteria for delisting, and estimates of the time and costs necessary to achieve criteria for delisting. Economists would favor recovery plans that achieve delisting criteria at a minimum cost. The general model we developed can be a useful tool in determining the optimal (least cost, present value) sequence of recovery actions for an endangered and threatened species when recovery actions are assumed to be integer variables.

We applied the general model to the recovery of the red-cockaded woodpecker in the Palmetto Peartree Preserve in North Carolina. The model specification included two integer valued recovery actions, the translocation of breeding pairs and the construction of artificial cavity clusters. The translocation of breeding pairs increased the number of breeding pairs in the population subject to a translocation success probability, while the construction of artificial cavity clusters directly increased environmental carrying capacity.

We used dynamic programming to find the optimal sequence of recovery actions that might achieve a population target over a given time horizon. For the deterministic model, it was possible to determine the feasible population targets, and a least-cost recovery plan could be found that precisely achieves each feasible population target in the deterministic model. A comparison of two least cost RCW recovery plans with different discount rates ($d' = 0.00$, $d' = 0.05$) demonstrated that discounting provides

incentive to delay implementing recovery actions. In our stylized stochastic instance (with a random variable drawn from a discrete distribution), it was not possible to guarantee that a population target could be reached with certainty. We solved the stochastic problem (with a stochastic map describing population dynamics) by specifying a penalty function where the population target serves as a kink separating the penalty line segment from the reward line segment.

The optimal recovery actions that solve our stochastic, optimization problem, comprise the adaptive, least cost recovery plan for the red-cockaded woodpecker population located in the 3P. In general, it is optimal to delay translocation of breeding pairs until later in the time horizon. Early in the time horizon, translocation is optimal only when the number of breeding pairs is small relative to the population target (Fig.2). However, later in the time horizon, translocation is optimal for all population levels except those that are equal to or exceed the population target. Early in the time horizon, artificial cavity cluster construction should be set to the maximum, except in the case that the number of breeding pairs is relatively small when compared to carrying capacity (Fig.3a). The explanation for this lies in how we modeled RCW population dynamics. Net natural growth is minimized when the ratio of breeding pairs to carrying capacity (N_t/K_t) is near 0 or 1 and net natural growth is maximized when the ratio of breeding pairs in the population to carrying capacity of population is equal to 0.5. In order to achieve and maintain this optimal ratio, optimal artificial cavity cluster construction should be implemented early in the time horizon. Later in the time horizon, the optimal recovery plan includes a positive level of artificial cavity cluster construction only in those instances where the number of breeding pairs is at or near carrying capacity.

Intuitively, the optimal decision rules for the RCW recovery actions make sense. Translocation is relatively expensive; therefore, with a positive discount rate, it is optimal to delay translocation (if possible) until later in the time horizon. As t approaches T , however, it is necessary to perform translocation to reach or exceed the population target in order to avoid incurring a penalty. If a population level is achieved that will reach the population target with high probability, however, there is no incentive to perform translocation because the benefit does not exceed the cost. Conversely, artificial cavity cluster construction is relatively inexpensive. Instead of delaying until later in the time horizon, it is optimal to construct artificial cavity clusters early in the time horizon. By constructing artificial cavity clusters to achieve a favorable ratio of breeding pairs to carrying capacity, the relative growth rate is increased. Maximizing the natural growth rate can help offset the need to perform expensive translocations. We can summarize the optimal decision rules as follows: if it is not possible to achieve the population target through an increase in carrying capacity, then it is necessary to resort to translocation.

The model used in the RCW problem specification does not account for the spatial attributes of a RCW population. Variables such as habitat type, habitat quality, proximity of adjacent territories, and the size and age-structure of individual breeding groups can all have an effect on the growth of a RCW population. Letcher et al. (1998) developed an individual-based, spatially explicit model of RCW population dynamics based on data from the Sandhills RCW population in North Carolina. This individual-based model accounts for the effects of artificial cavity construction on population dynamics, but does not account for translocation. Integrating an individual-based, spatially explicit model

with our approach would allow for more explicit modeling of RCW diffusion, but would greatly complicate the optimization problem.

APPENDIX A

In the stochastic problem, we used bilinear interpolation to assign a positive probability to the potential future states, $\lceil K_{t+1} \rceil, \lfloor K_{t+1} \rfloor, \lceil N_{t+1} \rceil$ and $\lfloor N_{t+1} \rfloor$ generated by the state transition functions (where $\lfloor x \rfloor$ is the largest integer less than x and $\lceil x \rceil$ is the smallest integer greater than x). We assign the probability of achieving state $\lceil K_{t+1} \rceil$ to be $\{K_{t+1}\}$, and the probability of achieving state $\lfloor K_{t+1} \rfloor$ to be $1 - \{K_{t+1}\}$ (where $\{x\}$ is the fractional part of a real number x). We use the same methodology to assign probabilities to $\lceil N_{t+1} \rceil$ and $\lfloor N_{t+1} \rfloor$. Because $(\lfloor K_{t+1} \rfloor, \lceil N_{t+1} \rceil)$ could result in an infeasible state (where $K_{t+1} < N_{t+1}$), we use $N_{t+1} = \min(N_{t+1}, \lfloor K_{t+1} \rfloor)$ to adjust N_{t+1} .

APPENDIX B

```

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%
%                               RCW Stochastic Dynamic Program
%
%                               Author: Ryan M. Finseth
%
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% Assign parameter values and initial conditions
alpha = .1;           % carrying capacity decay rate
m = 0;                % mortality
s = .25;              % translocation success prob
delta = .05;          % discount rate
rho = 1/(1+delta);    % discount factor
c2 = 800;              % cost of constructing one artificial cavity
c1 = 3000;             % cost of translocating one breeding pair
r = .13;              % intrinsic growth rate
K0 = 30;               % carrying capacity at t = 0
MAXK = 50;             % max carrying capacity
N0 = 20;               % number of breeding pairs at t = 0
T = 10;               % time horizon
X1MAX = 6;            % max number of translocations per year
X2MAX = 10;           % max number of artificial cavities constructed
NTstar = 42;          % population target
X2MIN = 0;            % min number of artificial cavities constructed
X1MIN = 0;            % min number of translocations per year
ep = [.75,1,1.25];    % matrix of epsilon values
ep_prob = [.25,.5,.25]; % probability of each epsilon value
R = 5000;              % final function 'reward' value
Q = 40000;            % final function 'penalty' value

%Calculate final function
COST = zeros(MAXK+1,MAXK+1,T+1);
OPTX1 = zeros(MAXK+1,MAXK+1,T);
OPTX2 = zeros(MAXK+1,MAXK+1,T);
CHECK = zeros(MAXK+1,MAXK+1,T+1);
n = 0;
k = 0;
while n <= MAXK
    while (k >= n && k <= MAXK)
        if n > NTstar
            COST(k+1,n+1,T+1) = (rho^T)*R*(NTstar-n);
        elseif n == NTstar
            COST(k+1,n+1,T+1) = 0;
        else
            COST(k+1,n+1,T+1) = (rho^T)*Q*(NTstar-n);
        end
        k = k+1;
    end;
    n = n+1;
    k = n;
end;

% Begin DP at the time t = T-1
t = T;
while t >= 1
    X1 = X1MAX;
    X2 = X2MAX;
    n = 0;
    k = 0;
    while n <= MAXK
        while (k >= n && k <= MAXK)
            % Generate state transition probabilities for all ep(j)
            num = length(ep);
            for j = 1:num
                if k == 0

```



```

        NT2(j) = ep(j)*(s*X1);
    else
        NT2(j) = ep(j)*((s*X1)+n+(r*n)-(m*n)-((r*n*n)/k));
    end;
    KT2(j) = ((1-alpha)*k) + X2;
    NT2_floor(j) = floor(NT2(j));
    NT2_ceil(j) = ceil(NT2(j));
    KT2_floor(j) = floor(KT2(j));
    KT2_ceil(j) = ceil(KT2(j));
    K1_cprob(j) = KT2(j) - KT2_floor(j);
    K1_fprob(j) = KT2_ceil(j) - KT2(j);
    N1_cprob(j) = NT2(j) - NT2_floor(j);
    N1_fprob(j) = NT2_ceil(j) - NT2(j);
    if KT2_ceil(j) == KT2_floor(j)
        K1_fprob(j) = .5;
        K1_cprob(j) = .5;
    end;
    if NT2_ceil(j) == NT2_floor(j)
        N1_fprob(j) = .5;
        N1_cprob(j) = .5;
    end;
    if KT2_ceil(j) > MAXK
        KT2_ceil(j) = MAXK;
    end;
    if KT2_floor(j) > MAXK
        KT2_floor(j) = MAXK;
    end;
    NT2_floor(j) = min(NT2_floor(j),KT2_floor(j));
    NT2_ceil(j) = min(NT2_ceil(j),KT2_ceil(j));
end;
% Compare expected costs of feasible recovery strategies
if (n + X1 <= k + X2)
    CHECK(k+1,n+1,t) = CHECK(k+1,n+1,t)+1;
    % Check if cost exists for state space combination
    if CHECK(k+1,n+1,t) == 1
        for j = 1:num
            excost(j) = ep_prob(j)*(((K1_fprob(j)*N1_fprob(j))*...
                COST(KT2_floor(j)+1,NT2_floor(j)+1,t+1))+...
                ((K1_cprob(j)*N1_fprob(j))*COST(KT2_ceil(j)+1,...
                NT2_floor(j)+1,t+1))+((K1_fprob(j)*N1_cprob(j))*...
                COST(KT2_floor(j)+1,NT2_ceil(j)+1,t+1))+...
                ((K1_cprob(j)*N1_cprob(j))*COST(KT2_ceil(j)+1,...
                NT2_ceil(j)+1,t+1)));
        end;
        % Assign cost and optimal recovery actions
        COST(k+1,n+1,t) = (rho^(t-1))*((c1*X1)+(c2*X2))+...
            sum(excost);
        OPTX1(k+1,n+1,t) = X1;
        OPTX2(k+1,n+1,t) = X2;
    else
        % Calculate expected cost
        for j = 1:num
            excost(j) = ep_prob(j)*(((K1_fprob(j)*N1_fprob(j))*...
                COST(KT2_floor(j)+1,NT2_floor(j)+1,t+1))+...
                ((K1_cprob(j)*N1_fprob(j))*COST(KT2_ceil(j)+1,...
                NT2_floor(j)+1,t+1))+((K1_fprob(j)*N1_cprob(j))*...
                COST(KT2_floor(j)+1,NT2_ceil(j)+1,t+1))+...
                ((K1_cprob(j)*N1_cprob(j))*COST(KT2_ceil(j)+1,...
                NT2_ceil(j)+1,t+1)));
        end;
        % Check to see if current recovery actions minimize
        if ((rho^(t-1))*((c1*X1)+(c2*X2))+sum(excost)) < ...
            COST(k+1,n+1,t)
            % Assign cost and optimal recovery actions
            COST(k+1,n+1,t) = ((rho^(t-1))*((c1*X1)+(c2*X2))+...
                sum(excost));
            OPTX1(k+1,n+1,t) = X1;
            OPTX2(k+1,n+1,t) = X2;
        end;
    end;
end;

```

```

end;
% Iterate through all recovery action combinations
X1 = X1-1;
if X1 < X1MIN
    X1 = X1MAX;
    X2 = X2-1;
    if X2 < X2MIN
        k = k+ 1;
        X1 = X1MAX;
        X2 = X2MAX;
    end;
end;
end;
% Iterate through all state space combinations
n = n+1;
k = max(n,1);
end;
% Decrease time step, loop until t < 0
t = t-1;
end;

```

REFERENCES

- Barlow, Z. 2008. Saving the California condors – slowly and at high cost. Scripps Howard News Service, Fillmore, California. Available from <http://www.scrippsnews.com/node/36392> (accessed September 2010).
- Baumgärtner, S. and M. F. Quaas. 2009. Ecological-economic viability as a criterion of strong sustainability under uncertainty. *Ecological Economics* **68**:2008-2020.

- Brown, G. M. and J. F. Shogren 1998. Economics of the endangered species act. *Journal of Economic Perspectives* **12(3)**:3-20.
- Clark, C. W., G. R. Munro, and U. R. Sumaila. 2010. Limits to the privatization of fishery resources. *Land Economics* **86(2)**:209-218.
- Conner, R. N., and D. C. Rudolph. 1989. Red- cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. USDA Forest Service Research Paper SO- 250. U.S. Department of Agriculture, Forest Service, New Orleans, Louisiana.
- Conner, R. N., D. C. Rudolph, D. L. Kulhavy, and A. E. Snow. 1991. Causes of mortality red-cockaded woodpecker cavity trees. *Journal of Wildlife Management* **55**:531-537.
- Conner, R. N., and D. C. Rudolph. 1995. Excavation dynamics and use patterns of red- cockaded woodpecker cavities: relationships with cooperative breeding. Pages 343- 352 in D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. *Red- cockaded woodpecker: recovery, ecology and management*. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas.
- Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. *The red- cockaded woodpecker: surviving in a fire- maintained ecosystem*. University of Texas Press, Austin, Texas.
- Conrad, J. M. 2000. Wilderness: options to preserve, extract, or develop. *Resource and Energy Economics* **22(3)**:205-219.
- Costa, R. and E. T. Kennedy. 1994. Red-cockaded woodpecker translocations 1989-1994: state of our knowledge. Pages 74-81 in *Annual Proceedings of the American Zoo and Aquarium Association*. Zoo Atlanta, Atlanta, Georgia.
- Daley, M. and J. Trevis. 2005. *Gray wolf management*. University of Minnesota Duluth, Duluth, Minnesota. Available from www.d.umn.edu/biology/courses/bio5865/documents/GrayWolfManagement.pdf (accessed September 2010).
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* **61(2)**:115-143.
- Edwards, J. and R. Costa. 2004. Range-wide success of red-cockaded woodpecker translocations. Pages 307 - 311 in *Proceedings of the 4th Red-Cockaded Woodpecker Symposium*. Savannah Georgia.

- Ferraro, P. J., T. Uchida, and J. M. Conrad. 2005. Price premiums for eco-friendly commodities: are 'green' markets the best way to protect endangered ecosystems? *Environmental and Resource Economics* **32**:419-438.
- Halsing, D. L. and M. R. Moore. 2008. Cost-effective management alternatives for the Snake River chinook salmon: a biological-economic synthesis. *Conservation Biology* **22**:338-350.
- Heppel, S. S., J.R. Walters, and L.B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. *Journal of Wildlife Management* **58(3)**: 479-487.
- Letcher, B. H., J. A. Priddy, J. R. Walters, and L. B. Crowder. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the red-cockaded woodpecker, *Picoides borealis*. *Biological Conservation* **86**: 1-14.
- Rudolph, D.C., R.N. Conner, and J.R. Walters. 2004. Red-cockaded woodpecker recovery: an integrated strategy. In: Costa, Ralph; Daniels, Susan J., eds. *Red-cockaded woodpecker: road to recovery*. Hancock House Publishers, Blaine, WA: 70-76.
- Shogren, J. F., et al. 1999. Why economics matters for endangered species protection and the ESA. *Conservation Biology* **13**:1257-1261.
- Tobin, A. J. and J. Dusheck. 2005. *Asking about life*. Brooks/Cole – Thompson Learning, Belmont, California.
- Tschirhart, J. 2000. General equilibrium of an ecosystem. *Journal of Theoretical Biology* **203(1)**:13-22.
- Underwood, E. C., M. R. Shaw, K. A. Wilson, P. Kareiva, K. R. Klausmeyer, M. F. McBride, M. Bode, S. A. Morrison, J. M. Hoekstra, and H. P. Possingham. 2008. Protecting biodiversity when money matters: maximizing return on investment. *PLoS ONE*, 3(1):e1515.doi:10.1317/journal.pone.0001515.
- USFWS (United States Fish and Wildlife Service). 1994. Whooping crane recovery plan. USFWS, Albuquerque, New Mexico.
- USFWS (United States Fish and Wildlife Service). 2003. Red-cockaded woodpecker recovery plan: second revision. USFWS, Atlanta, Georgia.
- USFWS (United States Fish and Wildlife Service). 2008. Florida panther recovery plan: third revision. USFWS, Atlanta, Georgia.
- Walters, J. R., P. D. Doerr, and J. H. Carter III. 1988. The cooperative breeding system of

- the red-cockaded woodpecker. *Ethology* **78**: 275- 305.
- Walters, J. R., S. J. Daniels, J. H. Carter, III, P. D. Doerr, K. Brust, and J. M. Mitchell. 2000. Foraging habitat resources, preferences and fitness of red-cockaded woodpeckers in the North Carolina sandhills. Fort Bragg Project Final Report. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, and North Carolina State University, Raleigh, North Carolina.
- Walters, J. R., L. B. Crowder, and J. A. Priddy. 2002. Population viability analysis for red-cockaded woodpeckers using an individual-based model. *Ecological Applications* **12**: 249- 260.
- Weitzman, M. L. 1992. On diversity. *Quarterly Journal of Economics* **107(May)**:363-406.
- Weitzman, M. L. 1993. What to preserve? An application of diversity theory to crane conservation. *Quarterly Journal of Economics* **108(Feb.)**:157-183.
- Weitzman, M. L. 1998. The noah's ark problem. *Econometrica* **66**:1279-1298.